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A RE-EVALUATION OF THE *HYLA BISTINCTA* SPECIES GROUP, WITH DESCRIPTIONS OF THREE NEW SPECIES (ANURA: HYLIDAE)

By

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Five stream-breeding tree frogs occurring in mountainous areas of Mexico were assigned to the *Hyla bistincta* group by Duellman (1964). Since that time, five species referable to this group have been described by Adler (1965), Duellman (1968), Straughan and Wright (1969), and Adler and Dennis (1972). Most of these species have relatively limited ranges in mountainous areas, and are allopatric. While working in Oaxaca, Mexico, in 1969-1970, I discovered three additional species referable to this group.

The five species included in the *H. bistincta* group by Duellman (1964) are *Hyla bistincta* Cope, *Hyla charadricola* Duellman, *Hyla robertsorum* Taylor, *Hyla pachyderma* Taylor, *Hyla crassa* (Brocchi). Duellman used the following combination of characters to separate this group from all other Middle American species groups: 1) absence of the quadratojugal, 2) non-projecting prepollex, 3) long fingers with little webbing, and 4) stream-inhabiting tadpoles having 2/3 tooth rows and two or more rows of labial papillae. Adler (1965) described *Hyla chryses* and *Hyla pentheter* and included them in the *bistincta* group; he recognized two subgroups. One subgroup is composed of medium-sized, slender, thin-skinned frogs

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without nuptial spines in breeding males, and with a distinct axillary membrane. These frogs occur at intermediate elevations, 2000-2600 m, in oak-pine forests of eastern Hidalgo, northern Puebla, and in central Guerrero. The second subgroup is composed of frogs which are medium to large, robust, and thick-skinned and which have nuptial spines on the first and second fingers of males but have no axillary membrane. These species are found at intermediate to high elevations (1600-3050 m) from Jalisco to Oaxaca and north to eastern Hidalgo.

Duellman (1968) described *Hyla siopela* from Cofre de Perote, Veracruz, México, and placed the seven species then known into three categories: 1) *bistincta* and *pentheter*—long anal sheaths; 2) *charadricola* and *chryses*—small species with axillary membranes and lacking nuptial excrescences in breeding males; 3) *crassa, pachyderma,* and *robertsorum*—short heads, round snouts, short anal sheaths, and nuptial excrescences in breeding males.

Hyla siopela was allocated to the last subgroup although it differs from the other three species included by the shape of the snout, and by the presence of a distinct rostral keel. Duellman also suggested that once the extent of the variation of these four species is known, they might represent a single species, although *crassa* has fully webbed feet and *pachyderma* has large nuptial spines.

Straughan and Wright (1969) named *Hyla bogertae* from the district of Sola de Vega in Oaxaca, and allocated it to Duellman's (1968) third subgroup. Duellman (1964, 1968) regarded *Hyla robustofemora* Taylor as a synonym of *Hyla crassa*, but Straughan and Wright considered *crassa* a *nomen dubium* until males and females from an extant population could be associated.

The tenth frog allocated to this group is *Hyla mykter,* described by Adler and Dennis (1972), who suggested that *mykter* is most closely related to *siopela.* Duellman's (1968) third subgroup, consisting of species typically found in moist oak-pine forests at intermediate to high elevations, was further subdivided by Adler and Dennis into two series: 1) those that are more robust and have more glandular skin, including *bogertae* (Oaxaca, 2650 m), *crassa* (Oaxaca, 2300 m), and *pachyderma* (Veracruz, 1600 m); and 2) those species that are less robust and have thinner skin, including *mykter* (Guerrero, 1985-2520 m), *robertsorum* (Puebla and Hidalgo, 2250-3100 m), and *siopela* (Veracruz, 2500-2650 m).

The purposes of this paper are to: 1) describe the three new species of tree frogs discovered in Oaxaca, and 2) to discuss phenetic similarities among these three new species, the other 10 species allocated to the *Hyla bistincta* group, and *Hyla arborescandens.* The *Hyla bistincta* group herein is divided into four species groups: 1) the *Hyla bistincta* group, 2) the *Hyla crassa* group, 3) the *Hyla charadricola* group, and 4) the *Hyla arborescandens* group (Table 1).

The phenetic relationships were determined by discriminant function and discriminant classification analysis. Comparisons of the different statistical methods are made and the advantages of each discussed. Results of the statistical analysis provide a different arrangement of species than the combination of characters used in the past to define subgroups within the *Hyla bistincta* group. The statistical results are considered preliminary because of the small number of specimens available of some species, and the consequent scarcity of morphological, skeletal, tadpole, and ecological data. Therefore, the definitions of the four new species groups are based on combinations of characters previously used by other workers.

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TABLE 1. Type localities, ranges, elevational limits, and habitats of the species presently included in the *Hyla bistincta* group and *Hyla arborescandens*. (See text for discussion of new species groups.)

	Type Locality	Range	Elevation	Habitat
Hyla bistincta species group				
Hyla bistincta Cope	"most probably Veracruz"	Mts. of Jalisco, Michoacán, México Morelos, Guerrero, Oaxaca	1400-2800	Pine, Pine-oak, and Pine-fir forests
Hyla pentheter Adler	Oaxaca: 37 km N San Gabriel Mixtepec	Mountain slopes of Sierra Madre del Sur in Oaxaca and Guerrero	1320-2000	Tropical deciduous and pine-oak forest
Hyla charadricola species group				
Hyla charadricola Duellman	Puebla: 14.4 km (by road) W Huachinango	Northern Puebla and eastern Hidalgo	2000-2300	Pine and pine-oak forest
Hyla chryses Adler	Guerrero: 45 km air-line WNW Chilpancingo	Type locality only	2540-2600	Oak-pine-fir cloud forest
Hyla sabrina Caldwell	Oaxaca: 15.8 km S Vista Hermosa	7.8-16.6 km S Vista Hermosa, Western slope of Sierra de Juárez in Oaxaca	1650-2020	Cloud forest
Hyla crassa species group				
Hyla crassa (Brocchi)	"Mexico"	Restricted area in mts. of central Oaxaca, ca. 10 kms NE Oaxaca	ca. 1850-2300	Dry pine forest
Hyla pachyderma Taylor	Veracruz: Pan de Olla (South of Tezuitlán)	Type locality only	1600	Cloud forest
Hyla bogertae Straughan & Wright	Oaxaca: 1.6 km S La Cofradia, in tributary of Río Átoyac	Type locality only	2650	Pine-fir forest

Hyla cyanomma Caldwell	Oaxaca: 1.2 km N Cerro Pelón, Sierra de Juárez	Type locality only	2650-70	Pine-oak forest
Hyla cembra Caldwell	Oaxaca: Campamento Río Molino, Sierra Madre del Sur	Type locality only	2160	Pine-oak forest
Hyla arborescandens species group				
Hyla arborescandens Taylor	Veracruz: 3 km SW Acultzingo	Sierra Madre Oriental from northern Puebla to central Oaxaca	1600-3100	Pine-oak forest; cloud forest
Hyla robertsorum Taylor	Hidalgo: El Chico Parque Nacional	Extreme northern Puebla and eastern Hidalgo	2550-3050	Pine-fir forest
Hyla siopela Duellman	Veracruz: west slope Cofre de Perote	Type locality and Cerro Pelón, Sierra de Juárez, Oaxaca	2500-2550 2650-70	Pine-oak forest Dry-pine forest
Hyla mykter Adler & Dennis	Guerrero: 11.4 km (by road) SW Puerto del Gallo	Vicinity of Cerro Teotepec in Sierra Madre del Sur	1985-2520	Pine-oak forest to cloud forest

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Materials and Methods

A total of 283 frogs, 103 adult females and 180 adult males (Table 2) was analyzed using several multivariate statistical methods. Thirty-two characters were recorded for each specimen. Fifteen morphometric characters (continuous variables) were measured to the nearest 0.1 mm using either dial calipers or an ocular micrometer on a dissecting microscope. The other 17 characters were coded. The 32 characters are:

1. Snout-vent length—tip of snout to vent.
2. Tibia length.
3. Radial-ulnar length—elbow to tip of disc of fourth finger.
4. Foot length—proximal edge of metatarsal tubercle to tip of disc of fourth toe.
5. Head width—width of head at widest point.
6. Head length—distance from end of skull at jaw to tip of snout.
7. Diameter of eye.
8. Diameter of tympanum.
9. Internarial distance.
10. Interorbital distance.
11. Eye to nostril.
12. Eye to tympanum.
13. Length of metatarsal tubercle.
14. Diameter of disc of third finger.
15. Diameter of disc of fourth toe.
16. Lateral view of snout—coded: truncate (1); round (2); sloping (3); acuminate (4); protruding (5).
17. Dorsal view of snout—coded: truncate (1); round (2); acuminate (3).
18. Rostral keel—coded: absent (1); weak (2); present (3).
19. Supratympanic fold—coded: absent (1); weak (2); present (3).
20. Tympanum—coded: concealed (1); partially concealed (2); distinct (3).
21. Skin—coded: smooth (1); weakly tuberculate (2); tuberculate (3).
22. Thoracic fold—coded: absent (1); weak (2); present (3).
23. Axillary membrane—coded: absent (1); present (2).
24. Tubercles on ventrolateral edge of forearm—coded: absent (1); present (2).
25. Wrist fold—coded: absent (1); weak (2); present (3).
26. Tarsal fold—coded: absent (1); weak (2); present (3).
27. Subarticular tubercles—coded: single (1); bifid and large (2); bifid and separate (3).
28. Amount of webbing (fourth toe)—coded: base of disc (1); middle of penultimate phalanx (2); base of penultimate phalanx (3); middle of antepenultimate phalanx (4); base of antepenultimate phalanx (5).
29. Coloration of venter—coded: no pigment (1); small amount of pigmentation (2); large amount of pigmentation (3).

30. Dorsal color pattern—coded: plain (1); weakly mottled (2); mottled (3); large spots (4).
31. Posterior surfaces of thighs (pigmentation)—coded: plain (1); weakly mottled (2); mottled (3).
32. Color of chin—coded: plain (1); weakly mottled (2); mottled (3).

Many characters traditionally used to define subgroups of the *Hyla bistincta* group are used in the statistical analysis. Characters not used in the statistical analysis generally fell into two categories: 1) subjective characters which are not easily quantifiable, such as degree of thickness of skin or robustness of limbs, and 2) characters which show no variation within a species.

Because of the small sample sizes of females in many species, males and females were analyzed together; therefore, characters specific to one sex were eliminated from the statistical analysis.

Several computer programs were used to examine the data. One of these (BMD07M; Dixon, 1970) is a discriminant classification analysis which calculates canonical axes (Anderson, 1958). Individual OTUs are projected on the first two canonical axes. Approximate ninety-five percent confidence circles can be drawn around the means by using a radius of $1.96/\sqrt{n}$ canonical axis units, and around the groups by using a radius of 1.96 canonical axes units (Seal, 1968:137). One disadvantage of this program is that the groups are plotted on only two axes. If three or more axes explain additional variation, programs other than BMD07M can be used to plot the groups on three axes. For this purpose I used a multiple discriminant function program (MULDIS) which is part of the NTSYS (Numerical Taxonomy System) package, a group of multivariate programs developed at The University of Kansas.

Using MULDIS, discriminant functions were first calculated using only those groups with sample sizes greater than five, thus eliminating five of the original fourteen species used as groups. Next, the same program was run using all groups regardless of sample size. Multiplying the discriminant scores from the first run by the table of means from the second run gives a matrix containing the means of all OTUs plotted on discriminant functions which were calculated using only groups with sample sizes larger than five. This matrix is then used to obtain a three-dimensional plot by a program called PROJ3D from the University of Kansas Computation Center Library. This program plots a perspective view of a three-dimensional scatter diagram. Another option of this program allows the shortest simply connected network to be superimposed on the plot to link up the points.

Because populations of *Hyla arborescandens* and *Hyla siopela* in Oaxaca are superficially so similar, these two species initially were examined by populations using the discriminant classification program, BMD07M. As discussed above, *Hyla arborescandens* has one of the largest ranges of all the species under consideration;

therefore, five populations from Oaxaca, Veracruz, and Puebla were used in the analysis (Table 2). In addition, a single specimen from Cerro Machin, Oaxaca, and the type specimen from Acultzingo, Veracruz, were entered as separate groups. Using an option of the program, these two specimens were not used in calculating the canonical axes, but were subsequently projected onto the axes. Specimens from the two known populations of *Hyla siopela* from Cofre de Perote, Veracruz, and Cerro Pelón, Oaxaca, were used. Localities and sample sizes of all groups are listed in table 2.

DESCRIPTIONS OF NEW SPECIES

Hyla cyanomma new species

Holotype.—KU 137014, adult female, from a mountain stream 1.2 km (by road) N Cerro Pelón, 2650 m, in cloud forest on a northern slope of the Sierra de Juárez, Distrito de Ixtlán, Oaxaca, México; obtained by Jan Caldwell on 5 April 1970.

Allotype.—KU 137032 from the same stream as the holotype, 0.9 km (by road) N Cerro Pelón, 2670 m; Jan Caldwell, 11 May 1970.

Paratopotypes.—KU 136997-137007, 137009-13, 137015-31, 137033-34, 21 females and 14 males, from the same stream as the holotype and the allotype, from 0.9 to 1.3 km (by road) N Cerro Pelón, 2650-2670 m; Jan Caldwell and Paul B. Robertson, 5 April-12 July 1970.

Diagnosis.—A large, robust frog assigned to the *Hyla crassa* group because it lacks a quadratojugal, has a short, round head, thick glandular skin, long, moderately robust fingers without webbing, webbing of feet extending to middle or base of penultimate phalanx of fourth toe, and partially or completely concealed tympanum. It can be distinguished from all other members of the group by its uniformly colored, olive-green dorsum which becomes pale blue on the flanks and posterior surfaces of the thighs. The eyes are pale blue, and many frogs in the series have a few tiny bright yellow spots on the dorsum. The only frog around in sympatry with *Hyla cyanomma* is *Hyla siopela,* which is slightly smaller (maximum snout-vent length 50.4 mm in females and 47.3 mm in males) has a dark and light brown mottled dorsum (in some, dorsum is leaf green), and a distinct rostral keel.

Description of holotype.—Adult female, nongravid, body robust, limbs stout. Snout-vent length 64.2 mm; tibia length 32.6 mm (50.8% of snout-vent length); snout rounded in lateral and dorsal profiles; nostrils not protruding, located closer to tip of snout than to eye; internarial distance 5.3 mm (24.1% of head width); loreal region concave, canthal ridge rounded, not prominent; top of head flat; lips thick, only slightly flared laterally; pupil of eye horizontally elliptical, diameter of eye 5.9 mm (27.6% of head width); eye slightly

TABLE 2. Number of males and females of each species of the *Hyla bistincta* group used in the statistical analysis. If a locality is not given after the name, specimens throughout the range of the species were used in the analysis.

Species	Males	Females	Total
H. arborescandens . . . W slope Sierra de Juárez, low elevations	10	14	24
H. arborescandens . . . W slope Sierra de Juárez, high elevations	10	22	32
H. arborescandens . . . Cerro Machín	1	0	1
H. arborescandens . . . Cerro San Felipe	5	2	7
H. arborescandens . . . Tezuitlán, Puebla	19	0	19
H. arborescandens . . . Acultzingo, Veracruz	16	3	19
H. arborescandens . . . type specimen, Acultzingo	1	0	1
H. siopela . . . Cofre de Perote	6	6	12
H. siopela . . . Cerro Pelón	23	7	30
H. sabrina	6	7	13
H. pentheter	29	2	31
H. robertsorum	15	12	27
H. chryses	2	1	3
H. charadricola	4	8	12
H. pachyderma	1	2	3
H. bistincta	22	3	25
H. bogertae	0	2	2
H. crassa	3	4	7
H. mykter	1	1	2
H. cyanomma	5	7	12
H. cembra	1	0	1
Totals	180	103	283

closer to tympanum than to nostril; palpebral membrane unpigmented; supratympanic fold moderately heavy, extending from corner of eye to insertion of forearm; tympanum small, visible although covered with skin; diameter of tympanum 1.4 mm (6.5% of head width), upper edge hidden by supratympanic fold. Tongue cordiform. Skin smooth, thick on dorsum, granular on chin, venter, posteroventral surfaces of thighs; axillary membrane present; thoracic fold weak. Cloacal opening directed posteroventrally at midlevel of thighs; cloacal sheath short; tubercles present below anal opening intergrading with those on posterior surfaces of thighs. Forearm heavy; wrist fold present; no row of tubercles along ventrolateral margin of forearms; fingers long, moderately slender; vestigal webbing present between fingers two and three, and three and four, but no webbing between thumb and second finger; fingers, in order of length from shortest to longest: 1-2-4-3; disc on third finger 2.5 times diameter of tympanum; subarticular tubercles round, except distal tubercles on fourth finger bifid; supernumerary tubercles present on proximal phalanges; palmar tubercle single, small, flat. Dermal fold present on heel; tarsal fold absent; toes long, moderately

slender; toes, in order of increasing length: 1-2-5-3-4; webbing extending from base of disc of first toe to base of penultimate phalange of second toe, from base of disc on third to base of penultimate phalange of fourth, from base of penultimate phalange on fourth to base of disc on fifth toe; outer metatarsal tubercle absent; inner metatarsal tubercle large, flat, oval; subarticular tubercles round except distal tubercle on fifth toe weakly bifid; indistinct supernumerary tubercles present on proximal phalanges.

Color (in alcohol) of dorsum dark metallic gray with few tiny white spots, paler gray on flanks and limbs; venter, chin, and posteroventral surfaces of thighs gray changing to pale tan on first three toes and webbing, first two fingers, axillary membrane, and anteroventral surfaces of thighs.

Color (in life) uniform olive-green on dorsum of body and limbs; few tiny, bright yellow spots on dorsum; olive-green fading to pale blue around vent and along outer edge of forearm and tarsus; venter and chin greenish-yellow; ventral surfaces of limbs to first three toes and first two fingers bright yellow-orange; outer toes and fingers greenish-yellow; iris pale bluish-gray (Pl. 1).

Variation.—The allotype is an adult male with snout-vent length 53.1 mm, enlarged non-projecting prepollex, and nuptial excrescences lacking; other characters and coloration are like those described for holotype. Among 22 adult specimens, snout-vent length is 51.9-64.5 mm ($\bar{x}$=57.6 mm, N=15 ♀ ♀), 51.6-56.0 mm ($\bar{x}$=53.8 mm, N=7 ♂ ♂). The smallest female and male collected have snout-vent lengths of 36.7 and 34.5 mm, respectively. Of 39 juveniles and adults, 13 (5 juveniles and 8 adults) have the tympanum completely concealed, whereas the diameter of the tympanum is 0.7-1.6 mm ($\bar{x}$=1.2 mm) in the other 26. Even in the latter specimens, the tympanum always is covered with skin, concealing the tympanic ring. The axillary membrane is absent in 13 specimens. The distal subarticular tubercle on the fourth finger is single in 16 specimens, bifid in 21, and divided in one. All males lack vocal slits and nuptial excrescences. Variation in color in a series of 11 adults (KU 136997-137007) is as follows: the dorsum is olive-green with few tiny yellow spots, changing to pale blue along outer edge of tarsus and forearm. The venter and chin are dark greenish-yellow, and the limbs are yellow-ochre with a varying amount of brown. The yellow is brightest on the webbing of toes and fingers, becoming yellow-orange in a few. The eyes are pale blue or bluish-gray.

Distribution.—The species is known only from the type locality, a moderate-sized stream in the Sierra de Juárez of Oaxaca, México, at elevations between 2650-2670 m.

Natural History.—Most specimens were collected between 5 April and 12 July 1970, from a moderate-sized stream in a pine-oak cloud forest; one was taken from approximately the same locality on

5 August 1965. The latter part of the dry season and the early part of the wet season occur in April, May, and June; thus, the stream was flowing well but was never torrential. At night the frogs were lying completely submerged on the bottom of large pools or at the edges of pools with only their heads above water. When frightened, they attempted to hide by moving to the deepest part of the pool or by going under large rocks in the pools. During the months of April, May, and June, 1-10 *Hyla cyanomma* were present in each large pool in the stream. On the night of 10 May, 68 frogs were observed within 0.1 km. The frogs were found by day near the same pools, usually sitting on rocks several centimeters above the water. The only other species of tree frog found at this locality, *Hyla siopela*, was found only at night sitting on leaves of terrestrial bromeliads, on branches above the stream, or on mossy rock walls.

The reproductive condition of 22 female *H. cyanomma* was examined. Based on the condition of the oviduct, seven of these specimens are juveniles, 10 subadults, and five adults. All adults are nongravid. No amplexing pairs or egg clutches were found during the observation period from April to July. Two tadpoles referable to this species because of their large size were collected in January. Apparently reproduction occurs at the beginning of the dry season, possibly in December or January.

Description of tadpole.—Two tadpoles, KU 139849, are presumed to be *Hyla cyanomma*. Both are in developmental stage 26 (Gosner, 1960), and have body lengths 20.4 and 20.2 mm, and total lengths 55.4 and 52.3 mm, respectively; description of larger specimen (Figs. 1A and 2A) is as follows: body depressed, flattened dorsally, 1.6 times as wide as deep, body nearly same width throughout its length; snout broadly rounded in dorsal view, round in lateral view; nostrils small, directed anteriorly; closer to eyes than tip of snout; eyes small, directed dorsolaterally, widely separated; spiracle sinistral, directed posterodorsally, located at point below midline slightly less than two-thirds length of body; caudal musculature moderately developed, tapering at midlength of tail and ending anterior to fin; dorsal caudal fin arches near end of tail; depth of dorsal and ventral caudal fins two-thirds of caudal musculature at midlength of tail.

Mouth ventral, small, half as wide as body at greatest width; lips infolded laterally; edge of lips bordered by single row of papillae; inner row of larger, irregularly spaced papillae; upper beak slender with very fine serrations, tapering slightly to form lateral processes; lower beak robust with slightly larger serrations; two upper and three lower tooth rows, all equal in length and extending nearly to edge of lips, second upper row interrupted medially.

Body dark gray dorsally, lighter on sides and snout; venter transparent; caudal musculature with irregular gray spots, absence of

spots forms tan stripe dorsolaterally; caudal fins opaque with irregular gray spots.

Etymology.—The specific name is from the Greek *kyanos* meaning blue and the Greek *omma* meaning eye, and is in reference to the blue eyes of this species.

Hyla sabrina new species

Holotype.—KU 137086, adult female, from a mountain stream 15.8 km (by road) S Vista Hermosa, 1990 m, in cloud forest on a western slope of the Sierra de Juárez, Distrito de Oaxaca, México; collected by Jan Caldwell on 12 June 1970.

Allotype.—KU 137067, from a mountain stream 11.9 km (by road) S Vista Hermosa, 1920 m; Jan Caldwell and Paul B. Robertson, 17 May 1970.

Paratypes.—KU 137044, 137053, 137059-60, 137064, 137066, 137069-72, 137076, 137085, 137087, 10 females and 3 males, from mountain streams, 11.1-16.6 km S Vista Hermosa, 1840-2020 m; Jan Caldwell and Paul B. Robertson, 23 November 1969, 17 July 1970.

Diagnosis.—*Hyla sabrina* is a small, slender-limbed member of the *Hyla charadricola* species group because it lacks a quadratojugal, has thin skin and an axillary membrane, lacks nuptial spines in breeding males, has long, slender fingers with no webbing, round to slightly pointed snout, tan venter with dark brown mottling and a mottled dorsum. It differs from *charadricola* by its smaller size and the absence of a tympanum and from *chryses* by coloration and absence of a tympanum. *Hyla charadricola* and *H. sabrina* are most alike in coloration, have a mottled green and darker green dorsum, with dull yellow or yellow-orange on the posterior and anterior surfaces of the thighs. *Hyla chryses* resembles these two in coloration when cold and sluggish, but when active is a golden yellow overlaid with small brown flecks and some indistinct green flecks (Adler, 1965). At night, *Hyla sabrina* may be a bright leaf green. *Hyla sabrina* is sympatric with *H. chaneque* and *H. arborescandens*. *Hyla chaneque* is much larger than *sabrina*, has a blotched dorsum and a tympanum. *Hyla arborescandens* is also larger, has a mottled dark and light dorsum, a distinct rostral keel, a tympanum and less webbing than *sabrina*. *Hyla sabrina* can be distinguished from *Ptychohyla ignicolor*, which occurs nearby, by the lack of webbing between the fingers and the absence of the tympanum.

→

Plate 1. Top.—*Hyla crassa* ♂ (KU 148699; 52.4 mm, SVL) from 1.9 km S El Estudiante, 1850 m, Oaxaca, México. × 1. Photo by William E. Duellman. Middle.—*Hyla sabrina* ♀ (KU 137083; 31.2 mm SVL) from 15.8 km S Vista Hermosa, 1990 m, Oaxaca, México. × 2. Photo by Jan Caldwell. Lower.—*Hyla cyanomma* ♀ (KU 137008; 55.3 mm, SVL) from 1.2 km N Cerro Pelón, 2650 m, Oaxaca, México. × 1. Photo by Jan Caldwell.

PLATE 1

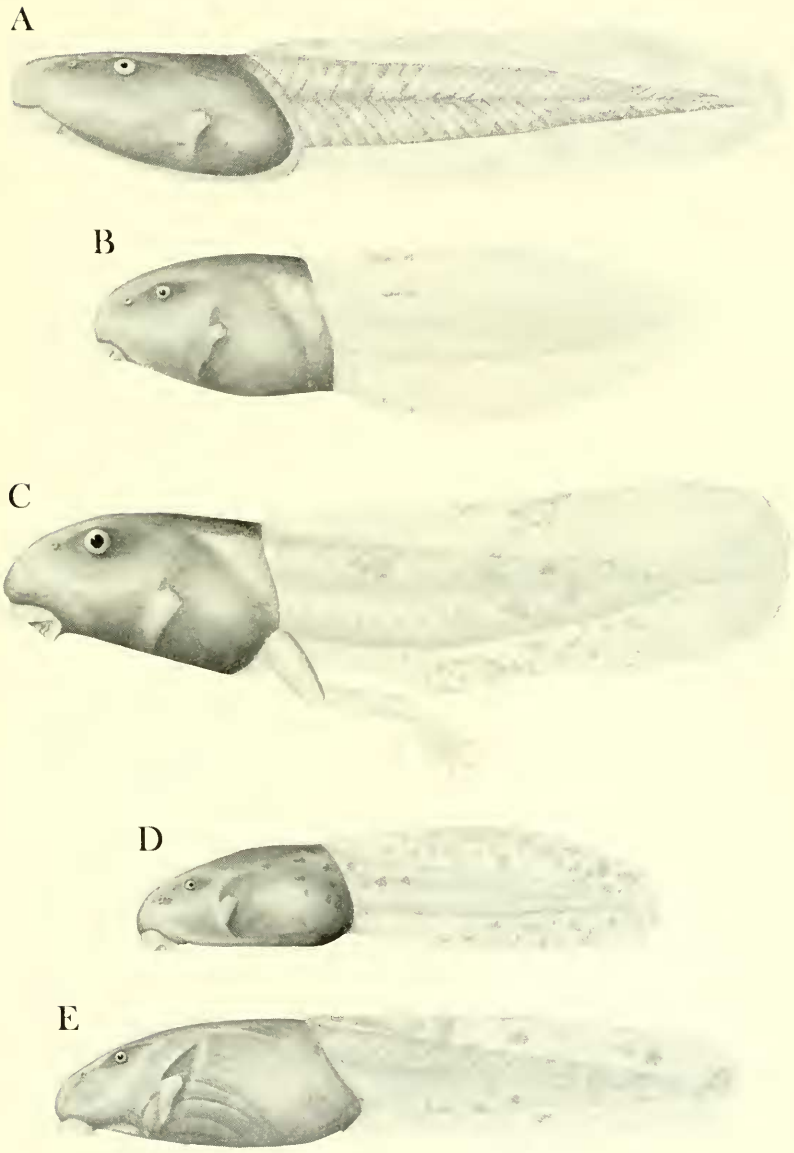

FIG. 1. Tadpoles of species in the *Hyla crassa* and *Hyla arborescandens* groups. A. *Hyla cyanomma*, KU 139849. B. *Hyla cembra*, KU 139859. C. *Hyla crassa*, KU 139845. D. *Hyla arborescandens*, KU 139832. E. *Hyla siopela*, KU 139841. × 2.

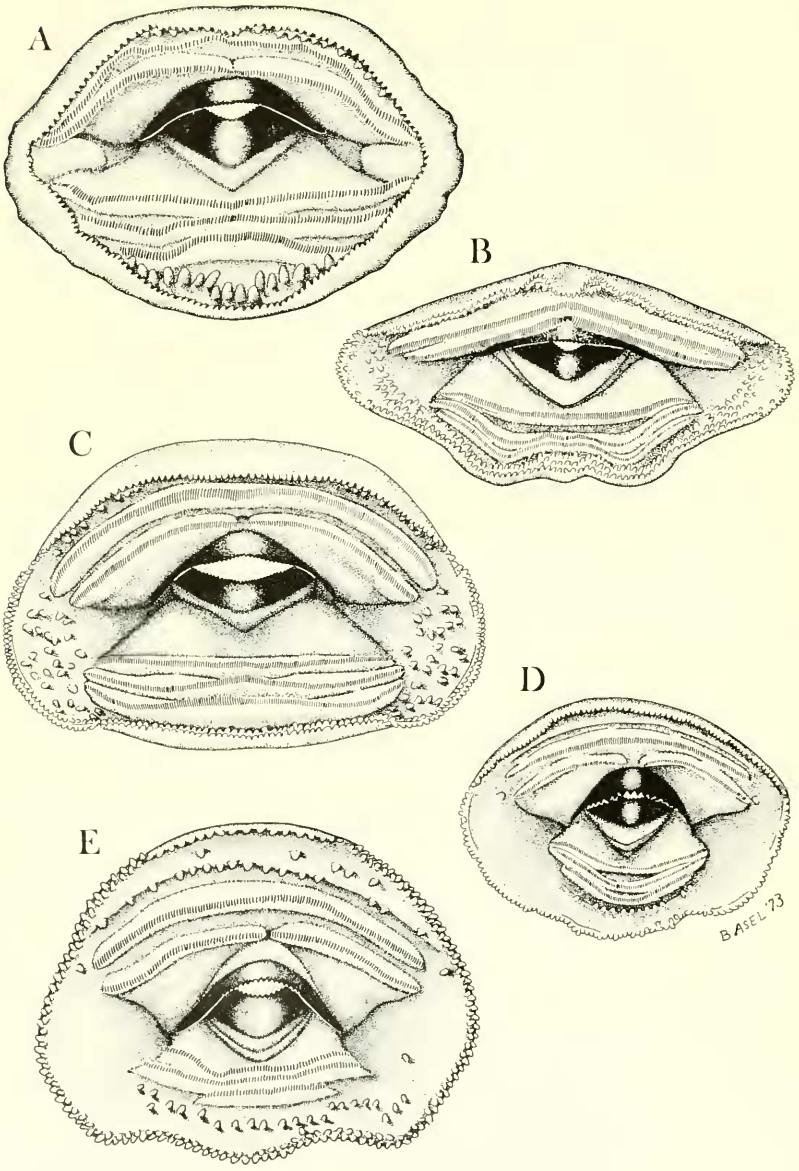

FIG. 2. Mouths of tadpoles of the *Hyla crassa* and *Hyla arborescandens* groups. A. *Hyla cyanomma*, KU 139849. B. *Hyla cembra*, KU 139859. C. *Hyla crassa*, KU 139845. D. *Hyla arborescandens*, KU 139832. E. *Hyla siopela*, KU 139841. × 10.

Description of holotype.—Adult female, gravid, medium-sized, slender-bodied. Snout-vent length 41.7 mm; tibia length 21.4 mm (51.3% of snout-vent length); snout in dorsal and lateral views acuminate; nostrils not protruding; internarial distance 2.9 mm (23.6% of head width), canthal ridge angular; loreal region flat; lips thin, not flared; pupil of eye horizontally elliptical; palpebral membrane unpigmented; diameter of eye 4.6 mm (37.4% of head width); supratympanic fold present, thin, extending from posterior corner of eye to forearm; tympanum absent; tongue round, posterior one-fourth free. Skin on entire body smooth, thin; few tubercles around vent; row of tiny white tubercles present on ventrolateral edge of forearm. Thoracic fold absent; small axillary membrane present. Anal opening directed posteroventrally at midlevel of thighs.

Forearm slender; prepollex only slightly enlarged; fingers, in order of increasing size: 1-2-4-3; subarticular tubercles round on distal articulation of three fingers, bifid on other three; few tiny supernumerary tubercles present on proximal phalanges; three palmar tubercles in a triangle at base of third and fourth fingers. Dermal fold present on heel; tarsal fold absent, indicated by a tiny row of white spots from heel to inner metatarsal tubercle; inner metatarsal tubercle small, flat, oval; outer metatarsal tubercle absent; subarticular tubercles small, round; few tiny supernumerary tubercles on proximal phalanges; toes, in order of increasing size: 1-2-3-5-4; toes approximately three-fourths webbed; webbing extending from base of first toe to middle of penultimate phalange of second toe, from base of second to base of penultimate phalange of third, from base of disc of third to base of penultimate phalange of fourth, from base of penultimate phalange of fourth to base of disc of fifth.

Color (in alcohol) gray on dorsal surfaces of head, body, and limbs with trace of mottling; white mottling where gray of dorsum meets dark brown of flanks and lateral surfaces of limbs; venter and ventral surfaces of limbs tan with overlying brown pigment.

Color (in life) light chocolate brown on dorsum with mostly green and some dark brown mottling; dark brown stripe extending from nostril along canthus to back of arm; green behind eye and below supratympanic ridge to upper lip; flanks dark brown, intergrading with light chocolate of dorsum, giving appearance of white mottling on flanks; anterior and posterior surfaces of thighs dull yellow, densely covered with brown; dull yellow extending on legs to first three toes, including webbing, and to first two fingers; dark brown around vent, with few tiny white tubercles; white line above vent; dark brown on ventrolateral edges of forearm, heel, and tarsus; rows of white tubercles on ventrolateral edge of forearm and outer edge of tarsus; venter tan with dark brown on chest, slightly lighter brown on throat; brown on ventral surfaces of legs; iris dark brown (Pl. 1).

Variation.—The allotype is an adult male with a snout-vent length of 29.8 mm, and an enlarged prepollex without nuptial spines. It has a round snout in contrast to the acuminate snout of the holotype; also, it has less brown pigment on the venter and chin than the holotype. Other characters and coloration in alcohol are as described for the holotype. Among the paratypic series of 13 adults, the snout-vent length for 10 subadult and adult females is 33.7-41.3 mm ($\bar{x}$=37.6 mm) and for 3 males is 26.9-29.9 mm ($\bar{x}$=28.2 mm). The smallest juvenile female and male collected have snout-vent lengths of 23.0 and 22.8 mm, respectively. Of the 10 females, 6 have venters and chins heavily pigmented, 3 lightly pigmented, and one has almost no pigment. Of the 3 males, one has venter and chin lightly pigmented and 2 have almost no pigment. Variation in color: KU 137051-52, dorsum mottled green, thighs dull yellow, flanks gray and white; KU 137063, dorsum mottled green, thighs light yellow, iris golden with black reticulations; KU 137038, dorsum mottled green and brown (bright green when first caught), flanks mottled brown and white, canthus dark brown with light gray line above, venter with dark brown pigment.

Distribution.—The species is known only from a restricted area in the cloud forest of the Sierra de Juárez. It has been taken from mountain streams 7.8-16-6 km (by road) S Vista Hermosa, 1650-2020 m.

Natural History.—All specimens were found on vegetation around fast-moving mountain streams. Of 33 females and 16 males collected throughout the year, only seven females and two males are adults. Two females, taken in June and July, are gravid. Tadpoles of this species are unknown.

Etymology.—The specific name *sabrina* is Latin meaning river nymph and refers to the aquatic habitat of this species.

Hyla cembra new species

Holotype.—KU 137035, adult male, from a mountain stream at Campamento Río Molino, 33.8 km (by road) N Candelaria Loxicha, 2160 m, in tropical deciduous forest in the Sierra Madre del Sur, Distrito de Pochutla, Oaxaca, México; collected by Jan Caldwell and Paul B. Robertson, 10 October 1969.

Diagnosis.—A moderate-sized, robust-limbed frog placed in the *Hyla crassa* species group because it lacks a quadratojugal, has robust limbs, a short, round head, thick, glandular skin, fingers long and moderately robust without webbing, webbing on feet extending to middle or base of penultimate phalange, and tympanum partially concealed. It differs from other members of the group, except *cyanomma*, by its uniform olive-green coloration and from *cyanomma* by its smaller size, lack of blue pigment on flanks or thighs and blue eyes. No tree frogs have been found in sympathy with *Hyla cembra*.

Description of holotype.—Adult male, body moderate in size, robust; snout-vent length 37.0 mm; tibia length 18.8 mm (50.8% of snout-vent length); snout rounded in dorsal and lateral profile; canthus rounded, indistinct; loreal region barely concave; lips moderately thick, not flared laterally. Pupil horizontally elliptical; palpebral membrane unpigmented. Dermal fold from corner of eye to insertion of forearm; upper edge of tympanum indistinct; tympanum small, 1.3 mm (10.9% of head width), tympanic ring barely visible. Tongue cordiform, barely free behind; vocal slits absent.

Skin smooth on dorsum of body and limbs, weakly granular on venter, chin, and ventral surfaces of thighs. Thoracic fold absent; axillary membrane present, but not extending to elbow; faint row of tubercles present on outer edge of forearm; wrist fold moderately developed; fingers long, not especially slender, in order of length from shortest to longest: 1-4-2-3; no webbing between fingers; discs moderate in size, that on third finger 1.4 times larger than tympanum; subarticular tubercles round, single except those on fourth finger bifid; supernumerary tubercles present, numerous; two moderately large palmar tubercles present; prepollex enlarged, nonprojecting, with numerous small nuptial spines; nuptial spines present on first and second fingers.

Length of foot 17.4 mm; discs small, about two-thirds those on fingers; subarticular tubercles round; supernumerary tubercles small, numerous. Webbing on foot extending from base of disc of first finger to base of penultimate phalange on second finger, from base of disc on second to base of penultimate phalange on third, from base of disc of third to base of penultimate phalange of fourth, and from the latter to base of disc on fifth; toes, in order of length from shortest to longest: 1-2-5-3-4, length of tibia 19.5 mm; heels overlap about one-third length of tibia; anal opening mid-level of thighs; transverse dermal fold above anus; few moderately large tubercles lateral and ventral to anus.

Color (in alcohol) uniform dull grayish brown on dorsum and upper surfaces of limbs; venter, anterior and posterior surfaces of thighs, first three toes and first two fingers light tan; moderately large tubercles lateral to anus dull yellow; nuptial spines dark brown.

Color (in life) bright greenish yellow on dorsum when first caught, later changing to dull green; light brown and green reticulations along sides; throat and chest white; ventral sides of limbs and belly pinkish tan; iris brownish yellow.

Natural History.—The single known specimen was found calling at night from under a piece of bark on a large log in a small stream. The call is a short "wrack" often followed by a series of low chuckles. Tadpoles, probably referable to this species, were common in streams in the area in April and July. No other tree frogs are known to occur in the area.

TABLE 3. Measurements (in mm) of *Hyla cembra* tadpoles in various stages (Gosner, 1960) from three localities. Single figure is the mean; range is given below in parentheses.

Stage	N	Body Length	Total Length
Campamento Río Molino, 2160 m			
26	2	12.6	30.0
		(11.5-13.7)	(29.2-30.8)
27	1	13.0	29.9
28	2	14.3	32.6
		(13.5-15.0)	(30.2-37.0)
29	1	14.8	----
30	3	15.7	39.7
		(14.6-16.6)	(38.0-41.3)
31	4	16.3	42.1
		(14.9-17.6)	(36.0-45.5)
33	2	16.4	42.5
		(15.8-17.0)	(40.4-44.6)
35	2	17.1	47.2
		(16.2-18.0)	(43.9-50.5)
36	1	16.3	----
11.6 km S Campamento Río Molino, 1970 m			
28	1	16.1	40.1
31	2	17.3	44.1
		(16.4-18.1)	----
37	1	19.2	----
38	1	18.4	----
12.8 km S Campamento Río Molino, 1930 m			
34	1	16.9	46.0
36	1	16.8	42.0

Description of Tadpole.—Twenty-five tadpoles from Campamento Río Molino, 2160 m, to 12.8 km S Campamento Río Molino, 1930 m, were collected. These tadpoles are assumed to be *Hyla cembra* because no other frogs have been observed or collected in this area. The body and total lengths are given in Table 3. The following is a description of a tadpole from Campamento Río Molino, KU 139859 (Figs. 1B and 2B), that is in developmental stage 30 (Gosner, 1960): body length 15.8 mm, total length 41.3 mm, tail slightly less than two-thirds length of body; body slightly depressed, nearly ovoid, depth 88 percent of width; venter flat, dorsal contour sloping anteriorly; snout broadly rounded in dorsal view, rounded in lateral view; nostrils small, directed anterolaterally, located halfway between tip of snout and eye; eyes moderately large, directed dorsolaterally, widely separated; spiracle sinistral, directed posterodorsally, located at a point on midline of body slightly less than two-thirds length of body; anal tube moderately long, dextral; caudal musculature moderately heavy, tapering gradually, ending anterior to caudal fin; dorsal and caudal fins normal, large; dorsal fin 1.1 times and ventral fin 1.2 times as deep as musculature at midlength of tail.

Mouth small, less than two-thirds width of body; lips infolded laterally; several irregular rows of papillae around edge of lips; papillae especially numerous on lower lip and lateral corners of lips; one regular row of slightly larger papillae medial to outer rows; beak moderate in size with very fine serrations; upper beak forms arch with long slender processes; two upper and three lower tooth rows; lower rows slightly shorter than upper, but all extending nearly to lateral edges of lips; second upper row interrupted medially.

Color (in alcohol) uniform dark brown on dorsum and sides; spiracle light gray; venter dark but transparent; caudal musculature light tan; caudal fins light transparent gray, plain except for few tiny brown spots on outer edge of fin.

Color (in life, taken from KU 139857) body dark brown covered with light green, yellow, and copper chromatophores; caudal musculature light yellow-brown; caudal fins same color as musculature with few light yellow and copper chromatophores; eye yellow.

Etymology.—The specific name *cembra* is Latin meaning timber and is used in reference to the pine-oak forest this species inhabits.

SYSTEMATICS

Re-evaluation of the *Hyla bistincta* group *(sensu lato)* has resulted in the allocation of these 13 species, plus *Hyla arborescandens*, into four groups, as defined and discussed below.

The Hyla bistincta Group

Content.—As redefined, the *Hyla bistincta* species group includes *Hyla bistincta* and *H. pentheter.*

Definition.—The species in this group are characterized by: 1) large body size, 2) truncate snout, 3) no quadratojugal, or small spine-shaped quadratojugal failing to articulate with maxillary, 4) distinct tympanum, 5) vocal slits present or absent, 6) breeding call present, 7) bold reticulated pattern on flanks, 8) plain dorsum, 9) venter plain, 10) thick skin, 11) long anal sheath, 12) nuptial spines on first and second fingers of breeding males, 13) long, slender fingers without webbing, 14) robust limbs, 15) webbing on feet extending to base of penultimate phalanx or to base of antepenultimate phalanx.

Distribution.—Hyla bistincta is the most widespread species of those included in the four groups (Table 1; see Duellman, 1970, for distribution map); it has an elevational range of 1400 to 2800 m. *Hyla pentheter* is confined to a more restricted area in the deciduous tropical forest in the mountains of the Sierra Madre del Sur in Oaxaca and Guerrero and has an elevational range of 1320 to 2000 m.

The Hyla charadricola Group

Content.—This group is composed of three species: *Hyla charadricola, H. chryses,* and *H. sabrina.*

Definition.—The following combination of characters separate this group from all other species groups: 1) small to medium body size, 2) snout round to slightly pointed, 3) no quadratojugal, 4) tympanum distinct, partially concealed, or concealed, 5) vocal slits absent, 6) breeding call absent, 7) fine mottling or spots on flanks, 8) mottled dorsum, 9) venter mottled dark brown and gray or tan, 10) thin skin, 11) transverse anal sheath, 12) nuptial spines absent in breeding males, 13) long, slender fingers without webbing, 14) slender limbs, 15) webbing on feet extending to base of penultimate phalanx or to base of antepenultimate phalanx.

Distribution.—The three species are allopratic and have fairly restricted ranges at moderate to high elevations. *Hyla charadricola* occurs in northern Puebla and eastern Hidalgo; *H. chryses* is known only from the type locality, 45 km (airline) WNW of Chilpancingo, Guerrero, and *H. sabrina* inhabits the Sierra de Juárez in Oaxaca. All have elevational ranges within 1650-2600 m.

The Hyla crassa Group

Content.—This group is composed of five species: *Hyla crassa, H. pachyderma, H. bogertae, H. cyanomma,* and *H. cembra.*

Definition.—These frogs possess the following combination of characters: 1) moderate to large body size, 2) snout round, 3) no quadratojugal, 4) tympanum partially or completely concealed, 5) vocal slits absent, 6) breeding call present or absent, 7) flanks plain or reticulated, 8) dorsum plain, flecked or spotted, 9) venter plain, 10) thick, glandular skin, 11) transverse anal sheath, 12) nuptial spines present on thumb and first finger (except *cyanomma,* but breeding season may have been past when males were collected) 13) long, moderately robust fingers without webbing, 14) robust limbs, 15) webbing on feet extending to middle or base of penultimate phalanx.

Distribution.—Each of the five species has a restricted distribution. *Hyla cembra* and *H. bogertae* occur in the Sierra Madre del Sur in Oaxaca, *H. cyanomma* in the Sierra de Juárez in Oaxaca, *H. pachyderma* in the Sierra Madre Oriental near Tezuitlán, and *H. crassa* in the central mountains of Oaxaca. The five species are allopatric and are found at relatively high elevations. With the exception of *Hyla pachyderma,* all are found in pine, pine-oak, or pine-fir forests between 1850 and 2650 m. *Hyla pachyderma* (known only from four specimens) was taken from cloud forest at 1600 m.

Remarks.—Three of the five species allocated to this group (*crassa, bogertae,* and *cyanomma*) are known to be highly aquatic in nature, and usually are found along streams sitting in water or

just above water. When frightened, these frogs hide in the water beneath rocks or other debris. Of the other two species, the four known specimens of *pachyderma* were found on bushes and weeds beside a small bounding stream (Taylor and Smith, 1945), and the single specimen of *Hyla cembra* was calling beneath the bark of a log in a stream.

As discussed above, Straughan and Wright (1969) regarded *Hyla crassa* a *nomen dubium* and continued to use *Hyla robustofemora*, although Duellman (1964) had compared the types of *Cauphias crassus* Brocchi and *Hyla robustofemora* Taylor and concluded that they represented the same species.

Five recently acquired specimens of *Hyla crassa* from 1.9 km S El Estudiante, 1850 m, Oaxaca, allow assessment of the variation in this species. I also have one specimen from 9 mi NE Oaxaca available for comparison. Duellman (1964) listed the following characters of the female *H. crassa* (type of *Cauphias crassus*) as differing from the male *H. crassa (H. robustofemora* Taylor): 1) the tympanum is completely concealed, 2) vomerine teeth are 8-7, compared to 5-5 in the male, 3) more cream-colored mottling on the flanks and posterior surfaces of the thighs, and 4) more distinct mottling on the throat.

The above four characters and snout-vent length are compared among the *Hyla crassa* I have examined in table 4. I have not seen the type specimen of *Cauphias crassus* (= *Hyla crassa*) but have relied on Duellman's (1964) description for comparative purposes. The variation in size, distinctness of the tympanum, and degree of mottling of flanks, posterior surfaces of thighs, and throat, among the five recent specimens encompass the two specimens originally discussed by Duellman (1964). Therefore, I concur with Duellman that *Hyla crassa* and *Hyla robustofemora* are conspecific.

Color notes from living specimens of *Hyla crassa* are: KU 148696, ♀, and KU 148697, ♂, have dorsum pale greenish-gray (in dark), changing to dark brown (in light); mottling along outer edge of forearm, sides and outer edge of leg same color as dorsum interspersed with pale green; venter bright yellow; yellow extending onto legs and arms and becoming darker; yellow on venter becoming cream-colored to pale green on chin with darker mottling; female has heavier mottling on chin than male; heavy pale green irregular stripe above and below vent; eyes copper with black reticulations. KU 148698, ♀, same as above, but dorsum has very distinct irregular dark brown spots (becoming lighter if animal is kept in dark) on lighter greenish-brown to brown background; spots always distinct whether frog kept in dark or light (Pl. 1). Ronald Altig, who collected the specimens, noted that the same frog can change from spotted to uniform coloration.

Two individuals were on rocks and sticks a few centimeters

TABLE 4. Comparison of certain characters among 8 specimens of *Hyla crassa*.

Mus. No.	Sex	SVL	Tympanum	Vom. Teeth	Color flanks, thighs	Color throat
UIMNH 25050[a]	♂	53.7	Concealed above	5-5	Scattered spots	Spots
MNHN 6331[b]	♀	53.7	Concealed	8-7	Mottled	Distinct mottling
KU 125354[c]	♀	61.4	Partially concealed	4-4	Plain	Weakly mottled
KU 148696[d]	♀	62.5	Partially concealed	4-2	Weakly mottled	Mottled
KU 148697[d]	♂	56.5	Partially concealed	3-4	Mottled	Weakly mottled
KU 148698[d]	♀	63.1	Concealed	2-3	Plain	Mottled
KU 148699[d]	♂	52.4	Partially concealed	3-3	Plain	Weakly mottled
KU 148700[d]	♀	56.9	Distinct	1-3	Plain	Mottled

[a] type specimen of *Hyla robustofemora*
[b] type specimen of *Caulhias crassus*
[c] collected by C. McClung, April, 1969
[d] collected by R. Altig, August, 1972

above the water along a large stream by day. Four were along the same stream at night. These frogs lack vocal slits, but make long, low calls.

By the process of elimination, three tadpoles from this area are presumed to be *Hyla crassa*. One specimen, KU 139850, from 6.3 km SE Ixtlan, 1910 m, is in developmental stage 36 (Gosner, 1960) and has a body length of 21.8 mm and a total length of 59.2 mm. Two other specimens, KU 139854, from 2.3 km E and 11.6 km NE Oaxaca, 1720 m, are in stage 41 and have body lengths of 19.7 and 18.9 mm and total lengths of 60.1 and 54.4 mm, respectively. The description of the latter specimen (Figs. 1C and 2C) is as follows: shape of body depressed, depth of body 79 percent of width; tail equal to two-thirds body length; in lateral profile body flattened dorsally, snout bluntly rounded; snout round in dorsal profile; nostrils directed anterolaterally, located closer to eye than tip of snout; eyes large, directed laterally, widely separated; spiracle sinistral, directed posterodorsally, located at a point on midline two-thirds of body length; left forelimb evident beneath spiracle; anal tube moderately long and dextral; caudal musculature massive, ending before tip of tail; dorsal and ventral caudal fins normal, narrow at midlength of tail, 59 and 48 percent depth of caudal musculature, respectively; fins becoming deepest on posterior fourth of tail.

Mouth ventral, small, approximately one-half body width; lateral folds present; double row of small papillae completely bordering lips, becoming numerous on lateral areas of disc; inner row of larger widely spaced papillae present; beak slender, broadly V-shaped, with very fine serrations, small notch on upper beak; two upper and three lower tooth rows, same length and extending nearly width of mouth; second upper row interrupted medially.

Color (in life) of dorsum brown with copper and light yellow chromatophores; tail musculature grayish; fin grayish, transparent; tail with large black spots and numerous copper chromatophores forming blotches; dorsum of legs pale yellow with brown markings; eyes copper.

Color (in alcohol) of body gray; caudal fin and musculature tan with irregular dark brown flecks and spots; legs light gray above, whitish below.

The Hyla arborescandens Group

Content.—Four species comprise this group: *Hyla arborescandens, H. robertsorum, H. siopela,* and *H. mykter.*

Definition.—This species group is distinguished by the following combination of characters: 1) moderate body size, 2) snout slightly rounded to truncate, 3) no quadratojugal, 4) tympanum distinct, 5) vocal slits present or absent, 6) breeding call present or absent, not necessarily correlated with presence or absence of vocal slits,

7) flanks mottled, 8) dorsum mottled or reticulated, 9) venter plain to strongly mottled, 10) thin skin, 11) long or short anal sheath, 12) nuptial spines present on thumb and first finger of breeding males, 13) long, moderately slender fingers with traces of webbing between two outermost fingers, 14) slender limbs, 15) webbing on feet extending to base of penultimate phalanx or to middle of antepenultimate phalanx.

Distribution.—Hyla arborescandens has a relatively large geographic range extending from the Sierra de Juárez in Oaxaca northwestward to the Sierra Madre Oriental in Puebla. *Hyla siopela* is known from two isolated mountain peaks: Cofre de Perote in the Cordillera Volcánica Transversal in Veracruz, and Cerro Pelón in the Sierra de Juárez of Oaxaca. *Hyla robertsorum* has been found in five localities in eastern Hidalgo and northern Puebla, and *Hyla mykter* is known from the vicinity of Cerro Teotepec in the Sierra Madre del Sur of Guerrero. The elevational range of *Hyla arborescandens* encompasses that of the other three species (Table 1).

Remarks.—Hyla siopela was discovered around a small stream on the west slope of Cofre de Perote, Veracruz, elevation 2500-2550 m (Duellman, 1968). In the description of this frog, Duellman stated that in structure and coloration *Hyla arborescandens* resembles *siopela*, but the former is smaller and males of *arborescandens* have vocal slits, whereas those of *siopela* do not.

While working in Oaxaca, I found an isolated population of *Hyla siopela* on the north slope of Cerro Pelón in the Sierra de Juárez at elevations between 2650 and 2670 m. Thus, the two populations of *siopela* are found in isolated mountain ranges separated by the Río Quiotepec.

Specimens of *Hyla arborescandens* have been taken from localities surrounding both populations of *Hyla siopela*. While working a transect from Tuxtepec, Oaxaca, to Cerro Pelón (0-3000 m), I commonly found *Hyla arborescandens* around mountain streams between 1610 and 2020 m. No frogs were taken from 2020 to 2650 m on the transect, because of a lack of suitable habitat. I originally identified the specimens from Cerro Pelón as *Hyla arborescandens* because of their similarity to the frogs occurring at lower elevations. Coloration and certain structural features, such as the presence of a rostral keel, are nearly identical in the two populations. Closer examination, however, revealed that specimens taken at Cerro Pelón lacked vocal slits, as did those from Cofre de Perote. Also, the size differences among the various populations were consistent (Table 5). An increase in size due to elevational effects was ruled out because of the size of the male *arborescandens* taken on Cerro San Felipe at an elevation of 2670 m. These specimens have vocal slits and are similar in size to the *H. arborescandens* occurring at lower elevations in the area of Vista Hermosa. Female *ar-*

TABLE 5. Size differences among populations of *Hyla arborescandens* and *H. siopela*. Single figure represents the mean; the sample size is below the range.

	Hyla arborescandens	
	Vista Hermosa (1610-2020 m)	Cerro San Felipe (2670 m)
Snout-vent length (males)	35.4 32.5-40.0 (N=20)	35.6 34.6-37.1 (N=5)
Snout-vent length (females)	42.7 39.0-46.4 (N=34)	48.9 48.8-48.9 (N=2)
	Hyla siopela	
	Cerro Pelón (2650-2670 m)	Cofre de Perote (2500-2550 m)
Snout-vent length (males)	43.4 40.4-47.2 (N=22)	43.6 40.8-45.5 (N=6)
Snout-vent length (females)	49.9 47.9-51.9 (N=5)	48.6 45.1-52.0 (N=6)

borescandens on Cerro San Felipe are much larger than males, but this could be a function of the small sample size available (N=2). Neither specimen is as large as the largest *siopela* female from either Cerro Pelón or Cofre de Perote.

Additionally, the dorsal color pattern of the two populations of *H. siopela* appears to be more variable than that in *H. arborescandens*. Duellman (1968) reported that the dorsal coloration of *H. siopela* from Cofre de Perote varied from pale green to olive-green with darker green or black flecks or reticulations. Variation in dorsal pattern of the specimens from Cerro Pelón is as follows: one specimen leaf green, another light green with brown mottling, another light brown with few brown flecks, and several mottled light and dark brown. In contrast, the *H. arborescandens* from lower elevations in the area of Vista Hermosa, Oaxaca, have much less variation in coloration, usually having the dorsum mottled with light and dark brown.

Tadpoles of *H. arborescandens* (Figs. 1D and 2D) from the Vista Hermosa area and of *siopela* from Cerro Pelón (Figs. 1E and 2E) are very similar in body shape, mouthparts, and other structural features. The primary difference is size of the serrations of the upper beak; those in *arborescandens* are peglike and are larger than the serrations on the lower beak, whereas those in *siopela* are smaller and equal in size on the upper and lower beaks. The tadpole figured by Duellman (1970:376-377) as *arborescandens* has equal-sized serrations on the upper and lower beak and an additional

TABLE 6. A comparison of size differences between populations of *Hyla siopela* tadpoles from Cofre de Perote and Cerro Pelón. The single figure is the mean; the range is in parentheses.

	Stage	N	Body Length	Total Length
Cofre de Perote				
	37	1	23.8	63.8
	41	3	19.4	60.9
			(18.3-20.9)	(60.0-61.8)
Cerro Pelón				
	26	4	16.1	39.0
			(14.1-18.9)	(36.8-46.6)
	27	3	17.6	42.3
			(16.0-18.7)	(39.0-44.1)
	28	3	17.4	44.8
			(15.4-20.0)	(41.5-50.0)
	30	1	16.9	43.1
	32	1	18.3	47.8
	33	1	16.0	42.3
	40	1	16.5	45.1

lower broken tooth row. It is possible that this tadpole could be that of *H. sabrina*.

A comparison of *Hyla siopela* tadpoles from Cerro Pelón and Cofre de Perote was made. Four tadpoles, all in advanced stages of development, are available from Cofre de Perote, and 15 lots of tadpoles are available from Cerro Pelón. The mouthparts of the tadpoles from the two populations are identical, as are other structural aspects such as depth of caudal musculature and fins, and coloration (see Duellman, 1970, for description and figures of *Hyla siopela* tadpoles from Cofre de Perote). The primary difference between the two populations of tadpoles is size. All but one of the tadpoles from Cerro Pelón are in earlier stages of development than the Cofre specimens. The largest Cerro Pelón specimen, in stage 40 (Gosner, 1960), has a total length of 45.1 mm, compared with three specimens from Cofre in stage 41, which have a mean total length of 60.9 mm. Table 6 presents a comparison of measurements of the four tadpoles from Cofre de Perote and selected developmental stages from Cerro Pelón.

Several hypotheses can be made regarding the differences in size of the tadpoles of the two populations. Perhaps there has been a reduction in size of the *H. siopela* tadpoles on Cerro Pelón due to competition with the larger, sympatric *H. cyanomma*. Two *H. cyanomma* tadpoles from Cerro Pelón are approximately the same size as the *H. siopela* specimens from Cofre de Perote. In developmental stage 26, the *H. cyanomma* tadpoles have a mean total length of 53.9 mm. There are no frogs sympatric with *H. siopela* on Cofre de Perote. Alternatively, differences in water temperature may af-

fect the size of the tadpole. This hypothesis was considered unlikely because the range in water temperature at Cerro Pelón for 12 collections of tadpoles was 10°C to 17.8°C (mean 13°C), and the water temperature at Cofre when the specimens were collected was 15.5°C. However, little is known about seasonal or daily variation of water temperatures, or about other physical or chemical factors at the two localities which may influence developmental rates in these tadpoles.

RESULTS AND DISCUSSION

In the initial discriminant classification analysis (BMD07M) using individuals of 5 populations of *Hyla arborescandens* and 2 populations of *Hyla siopela,* 90 percent of the total amount of variation is explained by the first three axes as follows: one, 53 percent; two, 25 percent; and three, 12 percent. The plot of individuals on canonical axes I against II (Fig. 3) shows an interesting grouping by locality rather than species. *H. siopela* (B on Fig. 3) from Cerro Pelón is closer to *H. arborescandens* from the surrounding localities of Vista Hermosa (C and D) and Cerro Machín (E) than to the other population of *H. siopela* from Cofre de Perote (A). Two other populations of *H. arborescandens* from Tezuitlán and Acultzingo (both near the Veracruz-Puebla border, but separated by about 130 km; G and H on Fig. 3) are closer to each other than to *H. arborescandens* from the Vista Hermosa localities. One deviation from this pattern is that specimens of *H. arborescandens* from Cerro San Felipe (in central Oaxaca; F on Fig. 3) are plotted closer to *H. arborescandens* from Puebla and Veracruz than to those from other localities in Oaxaca. This could be due in part to small sample size, because only a few specimens (Table 2) are available from Cerro San Felipe. Values of the F matrix indicate that all groups are significantly different ($\alpha = 0.05$) from each other except the populations of *arborescandens* from low and high elevations north of Vista Hermosa (C and D on Fig. 3) and populations of *arborescandens* from Tezuitlán, Puebla, and Acultzingo, Veracruz (different at 0.001 level; G and H on Fig. 3).

As discussed previously, the two most obvious characters separating *siopela* and *arborescandens* are larger size and absence of vocal slits (in males) of *siopela.* Presence or absence of vocal slits was not used as a character in the multivariate analysis, but the plot of individuals on canonical axes I and II (Fig. 3) may reflect a size trend. The four populations of *arborescandens* from Vista Hermosa, Tezuitlán, and Acultzingo are the smallest frogs and are grouped near the bottom of the plot. *Hyla siopela* from Cofre de Perote are the largest specimens and appear at the top of the plot.

All fourteen species under consideration were analyzed next using BMD07M, MULDIS, and PROJ3D. The populations of *Hyla*

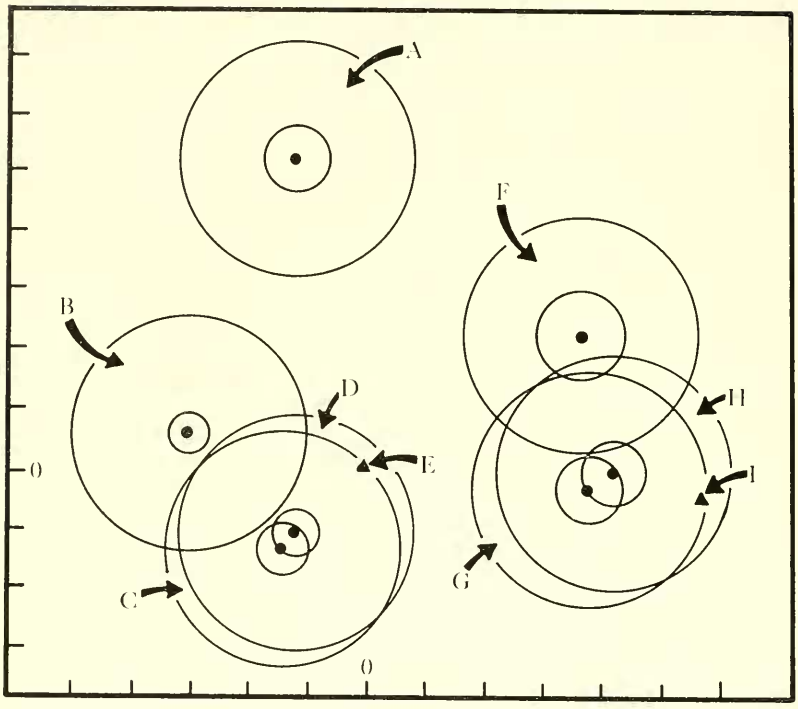

FIG. 3. Populations of *Hyla siopela* (A and B) and *Hyla arborescandens* (C-I) plotted on canonical axes I (horizontal axis) and II (vertical axis). Large circles are confidence circles around the groups; small circles are confidence circles around the means. Localities are as follows: A. Cofre de Perote, Veracruz. B. Cerro Pelón, Oaxaca. C. N Vista Hermosa, Oaxaca, low elevations. D. N Vista Hermosa, Oaxaca, high elevations. E. Cerro Machín, Oaxaca, (one specimen). F. Cerro San Felipe, Oaxaca. G. Tezuiltlán, Puebla. H. Acultzingo, Veracruz. I. Acultzingo, Veracruz (type specimen).

siopela and *arborescandens* discussed above were lumped for this part of the analysis. In addition to showing the interspecific relationships, results from BMD07M and MULDIS can be compared to show that additional information can be gained by examining plots with three axes rather than two.

Figures 4 and 5, from the BMD07M program, show the fourteen species plotted on canonical axes I and II. These two figures were made from the same graph and can be superimposed by aligning the zeros of each coordinate. The groups were separated for the figures by putting two species groups on each plot. Eight axes were required to explain the total amount of variation, with 81 percent explained by the first three axes, as follows: one, 41 percent; two, 30 percent; and three, 10 percent. The values of the final F matrix

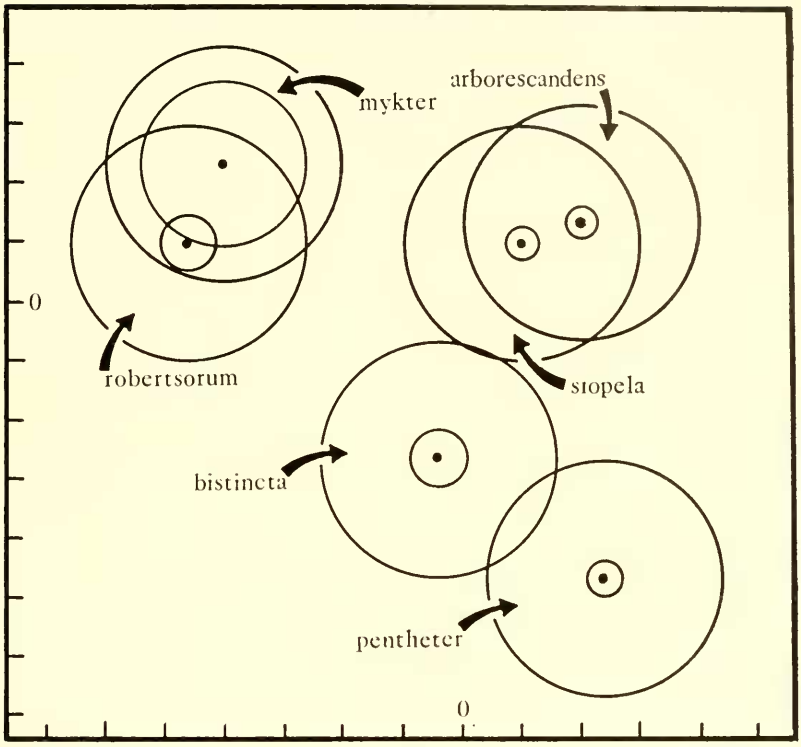

FIG. 4. Individuals of the *Hyla bistincta* group (includes *pentheter*) and the *Hyla arborescandens* group (includes *siopela, robertsorum,* and *mykter*) plotted on canonical axes I (horizontal axis) and II (vertical axis). Small circles are confidence circles around the means; large circles are confidence circles around the groups. This figure can be superimposed on Figure 5 by aligning the zeros of the coordinates.

indicate that all groups (species) are significantly different from all others.

Figure 4 includes the *bistincta* and *arborescandens* species groups, whereas figure 5 includes the *crassa* and *charadricola* species groups. Superimposing the two figures, the *bistincta* and *crassa* groups are most distinct, and the greatest overlap occurs between the *charadricola* and *aborescandens* species groups. In their original description of *mykter*, Adler and Dennis (1972) state that *mykter* appears to be related most closely to *bogertae, crassa, pachyderma, robertsorum,* and *siopela.* Superimposing the two figures, *mykter,* the first four aforementioned species and *sabrina* occur together in the upper left quadrat of the plot. Adler and Dennis further say that *mykter* is probably most closely related to *siopela,* which is not indicated by the graph. The following are four characters which Adler and Dennis use to indicate similarity between *mykter* and

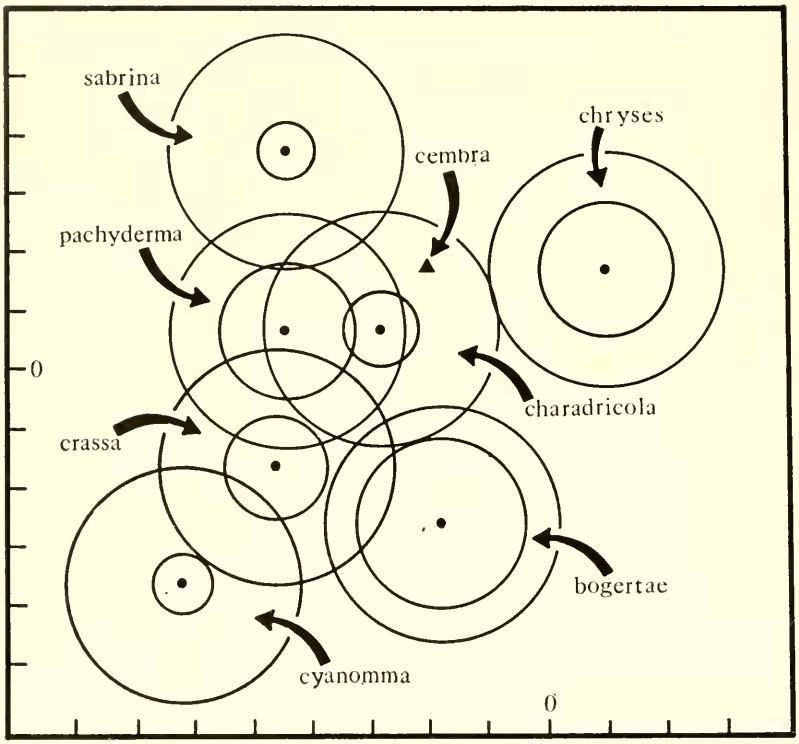

FIG. 5. Same as Fig. 4, but includes the *crassa* species group (*cyanomma, bogertae, pachyderma,* and *cembra*) and the *charadricola* species group (includes *chryses* and *sabrina*).

siopela: 1) rostral keel present; 2) traces of webbing between outer fingers; 3) thin skin; and 4) least robust bodies of the six species named above. Of these four characters, I used only the first in the multivariate analysis because the other three are not quantifiable. Adler and Dennis then list the following nine characters which differentiate *mykter* and *siopela:* 1) snout truncate in dorsal view in *siopela;* 2) snout truncate in lateral view of *siopela;* 3) canthus more angular in *siopela;* 4) nostrils of *siopela* more anterior; 5) nuptial excrescences present on first and second fingers of *siopela,* but on all fingers in *mykter;* 6) toes slightly more fully webbed in *mykter;* 7) cloacal sheath longer in *mykter;* 8) weak tarsal fold in *mykter;* and 9) proportionally longer legs in *mykter.* Of these nine characters, I used 6 in the multivariate analysis.

Adler and Dennis (1972) state further that of the four remaining species *(bogertae, crassa, pachyderma,* and *robertsorum), robertsorum* most closely approaches *siopela* and *mykter.* According to my analysis, *mykter* is closest to *robertsorum.* This is shown on both

TABLE 7. Distances of all species to all other species on the 3-dimensional plot obtained using PROJ3D (Figure 6). A, *H. siopela;* B, *H. arborescandens;* C, *H. sabrina;* D, *H. pentheter;* E, *H. robertsorum;* F, *H. chryses;* G, *H. charadricola;* H, *H. pachyderma;* I, *H. bistincta;* J, *H. bogertae;* K, *H. crassa;* L, *H. mykter;* M, *H. cyanomma;* N, *H. cembra.*

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
A	0	–	–	–	–	–	–	–	–	–	–	–	–	–
B	4.176	0	–	–	–	–	–	–	–	–	–	–	–	–
C	8.906	8.148	0	–	–	–	–	–	–	–	–	–	–	–
D	7.374	7.106	11.463	0	–	–	–	–	–	–	–	–	–	–
E	7.766	7.369	7.014	10.432	0	–	–	–	–	–	–	–	–	–
F	5.609	5.449	8.105	7.775	8.194	0	–	–	–	–	–	–	–	–
G	6.178	5.814	6.655	8.835	4.539	7.267	0	–	–	–	–	–	–	–
H	8.813	8.399	6.800	10.824	6.968	9.565	5.888	0	–	–	–	–	–	–
I	5.964	5.956	9.501	5.797	7.533	7.542	6.042	8.022	0	–	–	–	–	–
J	8.211	8.001	9.586	8.471	8.023	9.486	5.856	7.325	6.638	0	–	–	–	–
K	9.310	9.630	9.651	10.979	7.693	11.115	7.767	7.580	7.764	8.040	0	–	–	–
L	7.416	7.389	5.208	10.314	5.062	6.881	5.905	6.419	7.636	8.978	8.837	0	–	–
M	10.369	10.709	9.968	10.706	8.375	11.725	7.852	7.797	8.720	8.517	8.351	9.177	0	–
N	7.259	6.314	5.994	9.562	6.869	6.905	6.118	7.286	7.213	8.602	8.576	6.602	9.106	0

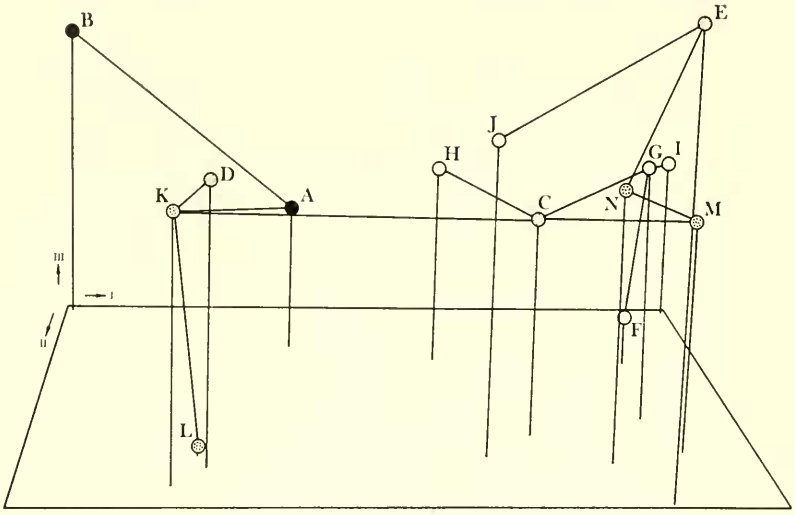

FIG. 6. A three-dimensional plot of the first three canonical axes from PROJ3D including all species originally in the *Hyla bistincta* species group and *Hyla arborescandens*. A. *Hyla bistincta*. B. *H. pentheter*. C. *H. charadricola*. D. *H. chryses*. E. *H. sabrina*. F. *H. crassa*. G. *H. pachyderma*. H. *H. bogertae*. I. *H. cyanomma*. J. *H. cembra*. K. *H. arborescandens*. L. *H. siopela*. M. *H. robertsorum*. N. *H. mykter*. Species groups indicated by symbols, as follows: closed circle, *Hyla bistincta* group; hatched line, *Hyla charadricola* group; open circle, *Hyla crassa* group; stippled circle, *Hyla arborescandens* group.

the two-dimensional and the three-dimensional plots. The three-dimensional plot (Fig. 6) shows that *mykter* is 5.062 units from *robertsorum* and 5.208 from *sabrina*. Table 7 presents the distances of all species from all other species, but figure 6 has lines drawn so that each species is connected to the one closest to it.

Straughan and Wright (1969), in their discussion of the relationships of these species, state that *siopela* is so superficially similar to *robertsorum* that they could be considered to belong to the same species population. The two characters they list which separate these two species are 1) the presence of the rostral keel in *siopela*, and its absence in *robertsorum*, and 2) the size of the bony prepollex element, which is twice as large in *siopela* as in *robertsorum*. My analysis reveals that *robertsorum* and *siopela* are not especially close. The two-dimensional plot (Figs. 4 and 5) shows *robertsorum* closest to *pachyderma*, *mykter*, and *charadricola*. The three-dimensional plot, however, shows that *robertsorum* is actually closest to *charadricola* (4.539 units) and is 6.968 units from *pachyderma*. This example also shows clearly the value of examining a three- rather than a two-dimensional plot.

Another interesting fact revealed by the three-dimensional plot is the relationship between *arborescandens* and *siopela*. The two-

dimensional plot (Fig. 4) shows the two overlapping to a great extent. However, figure 6 reveals that they are separated by a large distance (4.176 units) along the third axis. From the MULDIS program, the following combination of characters are found to contribute most significantly to the separation of groups along the third axis: 1) thoracic fold; 2) tubercles on lateral margin of forearm; 3) tarsal fold; 4) head width; and 5) snout-vent length. These characters are also important in separating *crassa* from *pachyderma.*

Regarding separation of groups along the first and second axes in the three-dimensional plots, the following combination of characters contribute most to separation along the first axis: 1) tubercles on lateral margin of forearm; 2) subarticular tubercles; 3) thoracic fold; 4) foot length; and 5) tarsal fold. The characters contributing most to separation along the second axis are: 1) tubercles on lateral margin of forearm; 2) color of dorsum; 3) pigmentation of thighs; 4) pigmentation of chin; 5) subarticular tubercles; and 6) thoracic fold.

The characters which I used initially to characterize the species groups are those which are easily observed in the field, and which other workers have considered important in the past. Some of these characters could not be used in the multivariate analysis as explained previously. However, the analysis has shown that, using 30 quantifiable characters, a somewhat different classification can be obtained. When more data are available, such as tadpole and skeletal data, and when larger samples of the adult frogs are available, we may find that another classification will more accurately represent phenetic relationships among these species.

SUMMARY

Five tree frogs were assigned to the *Hyla bistincta* species group by Duellman in 1964, and five more species were named and assigned to this group between 1965 and 1972. Three new species of tree frogs discovered in Oaxaca, Mexico, defined herein, are closely related to frogs of the *H. bistincta* group. The three new species are *Hyla cyanomma* and *Hyla sabrina* from the Sierra de Juárez, and *Hyla cembra* from the Sierra Madre del Sur.

The *Hyla bistincta* group is reviewed, and with *Hyla arborescandens,* is divided into four species groups, as follows: 1) the *Hyla bistincta* group, including *Hyla bistincta* and *Hyla pentheter,* 2) the *Hyla charadricola* group, consisting of *Hyla charadricola, Hyla chryses,* and *Hyla sabrina,* 3) the *Hyla crassa* group with *Hyla crassa, Hyla pachyderma, Hyla bogertae, Hyla cyanomma,* and *Hyla cembra,* and 4) the *Hyla arborescandens* group including *Hyla arborescandens, Hyla robertsorum, Hyla siopela,* and *Hyla mykter.* Characters used to define these new groups are those which have

been used in the past to delimit subgroups of the *Hyla bistincta* group.

Two multivariate statistical programs, discriminant classification analysis (BMD07M) and discriminant function analysis (MULDIS), are used to determine phenetic relationships among these 14 species. Comparisons of these statistical methods are made and the advantages of each discussed. The results of the statistical analysis provide a different arrangement of species than the combination of characters used in the past to define subgroups within the *Hyla bistincta* group. The statistical results are considered preliminary because of the small number of specimens available of some species, resulting in a deficiency of morphological, skeletal, tadpole, and ecological data. Therefore, the four new species groups are defined by characters used by previous workers.

RESUMEN

Cinco ranas fueron asignadas por Duellman en 1964 al grupo de especies *Hyla bistincta*, y cinco especies mas fueron denominadas y asignadas a este grupo entre 1965 y 1972. Tres nuevas especies de ranas descubiertas en Oaxaca, México, definidas aqui, están estrechamente relacionadas con ranas del grupo de *H. bistincta*. Las tres nuevas especies son *Hyla cyanomma* e *Hyla sabrina* de la Sierra de Juárez, e *Hyla cembra* de la Sierra Madre del Sur.

El grupo *Hyla bistincta* es revisado, y con *Hyla arborescandens*, es dividido en cuatro grupos de especies, a continuación: 1) el grupo *Hyla bistincta*, indugendo *Hyla bistincta* e *Hyla pentheter*, 2) el grupo *Hyla charadricola*, consistiendo de *Hyla charadricola*, *Hyla chryses*, e *Hyla sabrina*, 3) el grupo *Hyla crassa* con *Hyla crassa*, *Hyla pachyderma*, *Hyla bogertae*, *Hyla cyanomma*, e *Hyla cembra*, 4) el grupo *Hyla arborescandens* incluyendo *Hyla arborescandens*, *Hyla robertsorum*, *Hyla siopela*, y *Hyla mykter*. Las caractéres usados para definir estos nuevos grupos son aquellos que han sido usados en el pasado para delimitar subgrupos del grupo *Hyla bistincta*.

Dos programas de estadísticas multivariadas, análisis de clasificación discriminante (BMD07M) y análisis de funciones discriminantes (MULDIS), son usados para determinar relaciones fenéticas entre estas 14 especies. Comparaciones entre estos dos metodos estadísticos son hechas y las ventajas de cada uno son discutidas. Los resultados de estos análisis estadísticos producen una distribución de especies diferente a la combinación de caracteres usados en el pasado para definir subgrupos dentro del grupo *Hyla bistincta*. Los análisis estadísticos son considerados preliminares debido al pequeño número de especimenes disponibles de algunas especies, resultando en una deficiencia de datos morfologicos, de

esqueleto, de renacuajos, y ecológicos. Por lo tanto, los cuatro nuevos grupos de especies son definidos por caracteres usados por trabajadores anteriores.

SPECIMENS EXAMINED

Hyla arborescandens

OAXACA: Cerro San Felipe, FMNH 104575-78, UIMNH 27821-23, 30361, KU 137120-22, 139851-53 (tadpoles); Cerro Machín, UIMNH 50068-70; 3.5 km W Cerro Machín, 2370 m, KU 137119, 139837 (tadpoles); 15.8 mi SE Nochixtlán, UIMNH 38548; 32.5 mi NW Oaxaca, UIMNH 38546-47; 3.9 km S Vista Hermosa, KU 86994; 4.2 km S Vista Hermosa, 1580 m, KU 86999-7007, 139816 (tadpoles); 6.5 km S Vista Hermosa, 1610 m, KU 58453-3, 71216-20, 87008, 137123; 7.8 km S Vista Hermosa, 1650 m, KU 137124, 139817-19 (tadpoles); 9.1 km S Vista Hermosa, 1750 m, KU 137125-29; 9.3 km S Vista Hermosa, 1700 m, KU 137130-31; 9.4 km S Vista Hermosa, 1710 m, KU 139820-21 (tadpoles); 11.0 km S Vista Hermosa, 2070 m, KU 87012; 11.1 km S Vista Hermosa, 1840 m, KU 137132-35, 139822 (tadpoles), 139825-27 (tadpoles); 11.6 km S Vista Hermosa, 1870 m, KU 137136 (C & S), 139828-32 (tadpoles); 11.9 km S Vista Hermosa, 1920 m, KU 137137-42; 12.2 km S Vista Hermosa, 1920 m, KU 139834 (tadpoles); 12.3 km S Vista Hermosa, 1920 m, KU 137143-45; 14.3 km S Vista Hermosa, 1970 m, KU 137146; 15.0 km S Vista Hermosa, 1980 m, KU 104126 (tadpoles), 137147-51; 15.8 km S Vista Hermosa, 1990 m, KU 137152-76, 139835 (tadpoles); 16.0 km S Vista Hermosa, 2180 m, KU 87013-14; 16.6 km S Vista Hermosa, 2020 m, KU 137177-78, 139836 (tadpoles).

PUEBLA: 14.4 km W Huachinango, 2280 m, KU 58912; Paraja Verde, UIMNH 49119-20; Puente Colorado, UIMNH 49131; Río Octapa, 3.7 km NNE Tezuitlán, 1800 m, KU 53818, 55985, 58467-8, 64316-20, 68379-80 (tadpoles).

VERACRUZ: Acultzingo, FMNH 99261-2, 103285-6, 110596-8; near Acultzingo, UIMNH 27820, 27825-27, 49113-16; 0.5 mi above Acultzingo, FMNH 123916-19; 3 km SW Acultzingo, UIMNH 25045 (type); near Barranca, 1.2 mi SW La Joya, FMNH 70601-18, 70621-3, 70625-30; Barranca, 3 mi SW La Joya, FMNH 70624; La Joya, FMNH 70619-20; Pan de Olla, FMNH 125351-8, 172137-42, UIMNH 49117-18, 10135-49; 2 km N Paraja Nuevo, KU 23955; Pica de Orizaba, UIMNH 57635-84; Teocelo, Coscomatepec, Huatusco, KU 26846-50.

Hyla bistincta

GUERRERO: 4.5 km (by road) E El Limon (=6 km SW Chilapa), 1525 m, KU 140420-3.

MEXICO: W. Villa Victoria, UIMNH 29162.

MICHOACÁN: Uruapan, UIMNH 20457, 28167, KU 68077-8, 69093 (skeleton), UMMZ 112839 (14), 115233 (5); 14 mi from Rt 15 on Valle de Bravo Road, KU 148653.

MORELOS: 2 mi N Cuernavaca, UIMNH 28167.

OAXACA: Cerro San Felipe, UIMNH 28163, 56593, 59236-43, 60076-84, 62826-27, 73714-15, 73883-85, 73907.

SINALOA: 1 mi E Santa Lucia, 5650 ft, KU 44567.

VERACRUZ: Acultzingo, UIMNH 28164-66, 49133-34, 70188-91, 2 mi W Acultzingo, UIMNH 70192.

Hyla bogertae

OAXACA: Tributary of Río Atoyac, below Vivero El Tapanal, 1.6 km S La Cofradia, LACM 44400 (type), 44401-13, 44414 (tadpoles).